

## THE REPRESENTATION OF THE VISUAL FIELD ON THE CEREBRAL CORTEX IN MONKEYS

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On the basis of his extensive and elegant anatomical investigations on the visual cortex, Poliak (1932) suggested that a mathematical projection of the retina on the cerebral cortex must exist. Talbot & Marshall (1941) used physiological methods to map the central part of the visual field on to the posterolateral surface of the cortex in the monkey. They devised an index of cortical representation expressed as the increment of the angle, measured radially from the centre of gaze, which is represented on each millimetre of cortex. We have confirmed their observations and have extended the mapping to the buried visual cortex in the horizontal and vertical calcarine fissures. We have preferred to use the reciprocal of their index and to call it the cortical magnification,  $M$ . When this is measured along radii and at right angles to them, it provides the empirical quantitative relation which Polyak wanted. It also defines the shape and size of the visual receptive field. We have made such a surface, folded it and compared it with the calcarine cortex of the monkey. A preliminary account of this work has been published (Daniel & Whitteridge, 1959).

### METHODS

Out of twenty-two monkeys and baboons, we have had satisfactory records from the posterolateral surface of the cortex in fourteen, from the cortex of the calcarine fissure in eight. The first satisfactory experiments were carried out in 1952, but subsequently there were a number of unsuccessful experiments due to haemorrhage and to prolonged lowering of the blood pressure by pentobarbitone. The last eight experiments on three baboons, three large macaques, a cynomolgus and a vervet monkey have all been successful. We have found operation on small macaques very difficult, as unavoidable blood loss on opening the skull is liable to cause serious lowering of the blood pressure. We have been careful to induce anaesthesia slowly, using Dr C. G. Phillips's method of putting the animal in a small cage in a glass-fronted tank and pumping in nitrous oxide. The moment the animal appears to be unconscious, we have taken it out, given Nembutal (sodium pentobarbitone; Abbott Laboratories) 40 mg/kg, or hexobarbitone intraperitoneally, or chloralose 50–60 mg/kg intravenously. The animal is then put back into the small cage in room air and, after recovering from the nitrous oxide, it quietly becomes drowsy without further handling. In

one experiment in which the bone over the visual cortex was removed at a preliminary operation with aseptic precautions, the monkey readily entered the small cage 2 days later.

Chloralose was used in the last four experiments. No differences in the extent of the responsive area with barbituates and with chloralose have been observed, but the cortex has been in better condition and the blood pressure consistently higher with chloralose. Blood pressure was checked at intervals by means of a cuff on the tail or thigh, with a microphone to detect pulsation. A saline drip was given and, if necessary, 'Dextran' was given intravenously to maintain circulating fluid volume.

The bone over the posterior half of the left hemisphere was removed, giving an exposure from the posterior pole to the central sulcus, and from the mid line as far laterally as possible. The dura was opened under liquid paraffin.

The eye was fixed by four sutures through the limbus, which attached it to a brass ring which enabled it to be moved about. The head was fixed by ear clamps and a jaw piece to a stereotaxic machine, and the Clarke-Horsley plane was levelled with a spirit level in the usual way. In experiments since 1958, in addition to a general anaesthetic the monkey was given tubocurarine 0.2 mg/kg i.v. with artificial respiration, as no other way of preventing eye movements was found to be completely effective. Each animal was kept under full anaesthesia for up to 18 hr, when it was killed by an overdose of pentobarbitone and the brain perfused with 10% formol in NaCl solution 0.9 g/100 ml. The brain was removed on the following day, fixed for 3 weeks in 10% formol, embedded in low-viscosity nitrocellulose and cut serially at 100  $\mu$ . Sections were stained with Weil's method for myelin and photographed at  $\times 7.5$  or  $\times 10$ .

The stereotaxic machine was arranged so that the right eye was at the centre of an Aimark perimeter whose arm had a diameter of 33 cm. The eye was roughly centred by determining the optic axis by the reflexion of an image from the centre of the cornea. This does not, however, determine the visual axis, which is usually about 5° to the nasal side. In the later experiments one electrode was placed on the most lateral and anterior part of the superficial visual cortex and left there throughout the experiment. The eye was then moved by its ring until a light at the centre of the perimeter gave the largest and earliest response obtainable from this electrode. The animal was then given tubocurarine (in the later experiments). Before every observation with an exploring electrode the response from a central light was checked with the fixed electrode. The results of Talbot & Marshall (1941) and our own agree that the fovea is represented at the anterolateral corner of the visual area. As at this point 1° of the visual field is represented over nearly 6 mm of cortex, a minor displacement of the fixed electrode is of little importance during experiments with the peripheral field. The cornea was kept moist, but no contact lens was used.

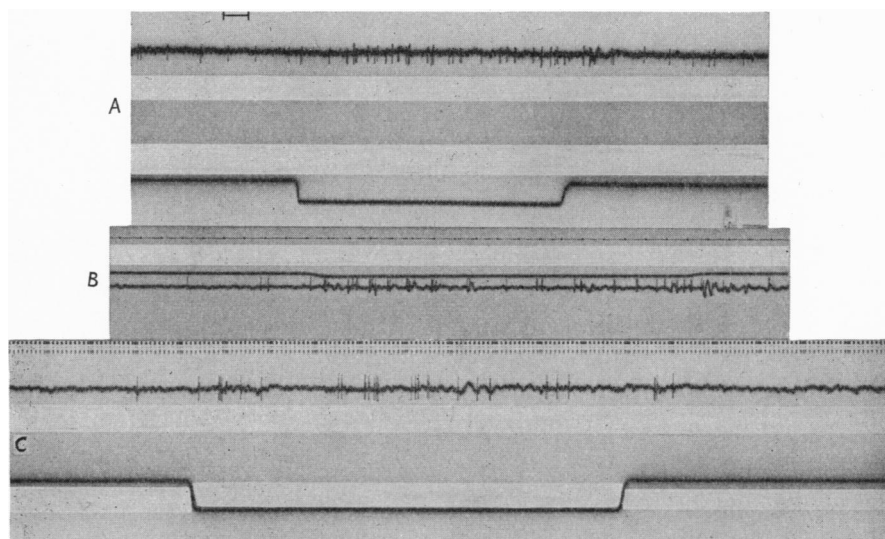
As electrodes we have used steel needles with shafts of 500  $\mu$  diameter with a long taper to less than 10  $\mu$ . Such needles leave easily recognized tracks. In this work it was essential to plot as many responses as possible in each experiment, and therefore no systematic attempt was made to record from single units. Instead, we have mapped the centre of the area on the perimeter which gave, from the recording electrode, the largest response of shortest latency. When responses from the same cortical point were repeatedly mapped in the dark, they agreed within 1°. Responses from the same cortical point recorded more than half-an-hour apart agreed to within 1°.

The perimeter gave white round illuminated patches of 38 cd/m<sup>2</sup>. The area illuminated was approximately a circle whose diameter could be varied from 1 to 10 mm. A transistor photocell excited from the light beyond the shutter provided synchronization of the cathode-ray tube sweep with 'off' and 'on' illumination, but for searching the field a neon tube 5 mm in diameter was used, which flashed for about 5 msec every 2 sec and was triggered from the sweep. This provided too much light for exact localization, and final mapping was done with a light spot of 1 mm diameter which subtended 10' at the eye, illuminated by 0.38–3.8 cd/m<sup>2</sup>.

## RESULTS

*Gross anatomy*

There seems to be very little difference between the calcarine areas in the brains of *Macacus rhesus*, *M. cynomolgus* and the vervet monkey. The baboon has a larger brain, and the calcarine cortex is further from the surface than it is in the macaque, but the general arrangement of the calcarine cortex seems to be the same. Though no electrical recording has



Text-fig. 1

A. Increase in a resting discharge in a cortical unit during 'on'. Time marker, 100 msec.

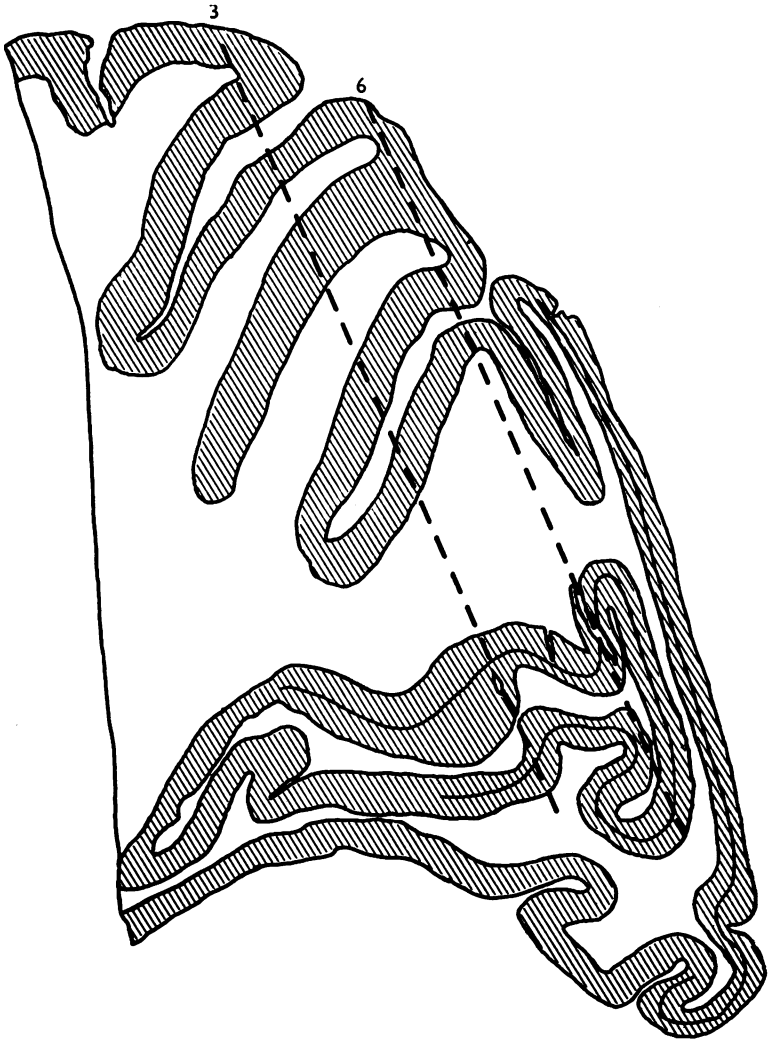
B. A number of units from the cortex of a rhesus monkey, 9-7-53. 'On'-effects have a latency of 30 msec.

C. 'On'- and 'off'-effects, and an irregular 'on'-discharge in a cortical single unit. Time marker, 1/100 and 1/10 sec. Signal falls at 'on'.

been done on the squirrel monkey and the pigtailed monkey, sections of visual cortex have been examined and show much the same arrangement as in the macaque. On the other hand, the spider monkey, *Ateles*, has much less of the macular cortex visible on the postero-lateral surface, and whereas the vertical limbs of the calcarine fissure lie in the same straight line in the macaque, they form an acute angle with each other in the spider monkey. On these points Polyak (1957) is very informative.

We have little to add to the description by Talbot & Marshall (1941) of the superficial visual cortex. The anterior boundary of the optically

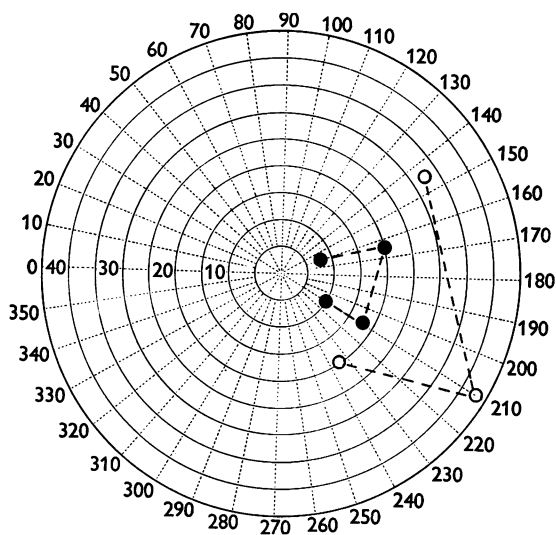
excitable cortex runs 1–2 mm posterior to the large vein that marks the lunate sulcus. A shallow sulcus is constantly seen in sections in the lower part of this area, but it is sometimes difficult to remove enough bone to expose this sulcus at operation. On the medial surface of the brain the calcarine fissure has a  $\neg$  shape, with a horizontal and two vertical limbs.



Text-fig. 2A

Parasagittal section of the occipital region of a baboon's brain. Cortex identifiable as area 17 is marked by a black line. In the stem of the 'mushrooom' there are four needle tracks made by needles slightly oblique to the plane of the section. Two of the tracks, 3 and 6 of the series, have been shown as though projected on to the plane of the section (cf. Text-fig. 2B).

This surface has not been explored under direct vision, but histologically area 17 surrounds the vertical limbs of the fissure and forms a narrow band on each side of the more posterior part of the horizontal limb. In sagittal section the calcarine cortex has the shape of a mushroom, with a 'head' and a 'stem'. In sections further from the mid line the 'head' gets smaller, and the most lateral sections show a 'stem' only, frequently cut obliquely (Pl. 1; Text-figs. 2, 3 and 7). The 'head' is frequently asymmetrical about the 'stem' of the calcarine cortex, with the lower part of the 'head' smaller than the upper part. Consistently with this, extra folds of the cortex on the lower wall of the 'stem' of the calcarine fissure are not uncommon. It therefore happens sometimes that area 17 is only found in the upper wall of the 'stem' of the calcarine fissure in the more medial sections.



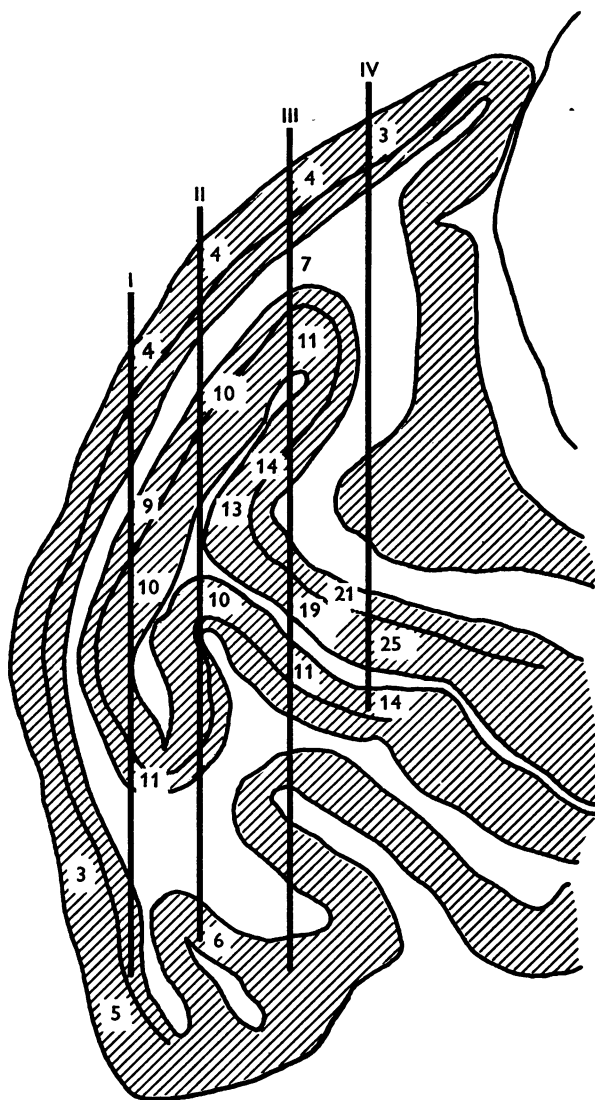
Text-fig. 2B

The responses in the visual field from track 3, ○; and from track 6, ●. Owing to the S bend of the 'stem' of calcarine cortex, track 3 gives responses of three points. Track 6 which crosses the head of the 'mushroom' gives responses from four points.

### *The physiological responses*

We have recorded responses from the exposed cortex with a silver ball electrode 2 mm in diameter; from the deeper layers with stainless-steel needles of 5–10  $\mu$  tip, and in later experiments with needles whose tips, produced electrolytically, were not more than 1–2  $\mu$ .

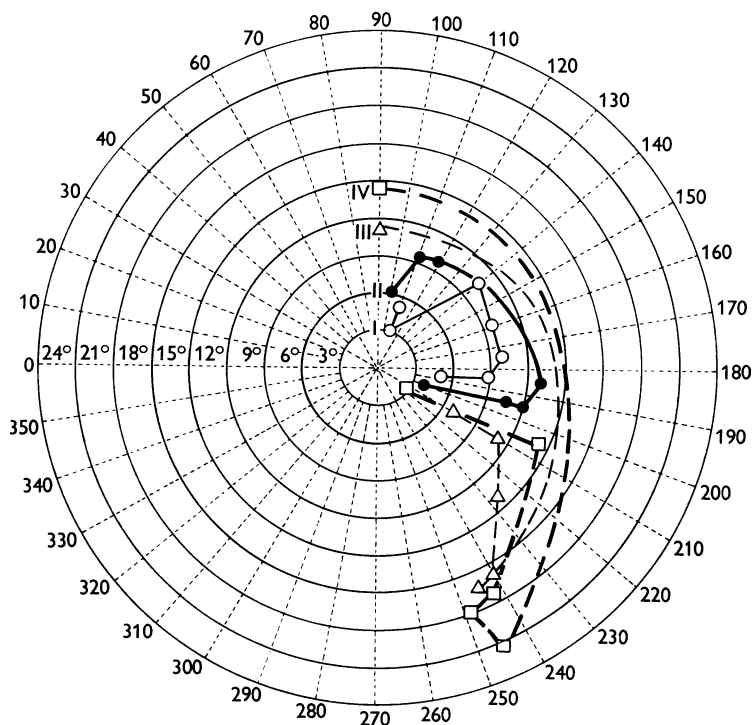
The silver ball regularly gave a response from the cortex, consisting of an earlier and a later wave, with latencies of 30–60 msec and about 100 msec. When the cortex was in good condition, the first wave could be localized to less than 1° on the perimeter, but if the amplitude of the response fell,



Text-fig. 3A

A parasagittal section of the occipital region of a baboon's brain, with four needle tracks projected on to it. The figures beside the tracks refer to the radial distance from the fixation point in degrees. Note that the upper lip of the calcarine fissure is concerned with points considerably further from the fixation point than is the lower lip. There is one minor inconsistency; 14° on track 3 should be somewhat lower to correspond with adjacent points (cf. Text-fig. 3B).

the point of maximum amplitude of the first wave was not distinguishable over about  $3^\circ$ . With the very fine needles the activity of cells and fibres could readily be recorded and occasionally large single units were obtained. No method has been devised which would permit of immobilization of the cortex over the  $4\text{--}6\text{ cm}^2$  needed for mapping, and it has not yet been possible to map systematically using single units. Further, the amount of detail provided by a fine electrode makes mapping so slow that it is un-



Text-fig. 3B

The corresponding points in the visual field. All four needle tracks give at first responses between  $5$  and  $3^\circ$  out. The roman figures are placed against their last responses, in each case in the upper visual field.

likely that enough points could be dealt with in one experiment. We have found that needles of  $5\text{--}10\ \mu$  tip give large waves whose components can be easily identified and usually allow one to distinguish white and grey matter.

With a steel electrode in the surface layers of the calcarine cortex a visual response was recorded at about  $0.2\text{ mm}$  below the surface. This could be obtained from an area on the perimeter of about  $10^\circ$  in diameter with the neon lamp. Using white light and reducing the area illuminated

to  $10^\circ$  and the intensity by one or two log. units, we could obtain a response from an area of about  $2-4^\circ$  diameter. These were multiple-unit responses. When the needle was in the calcarine fissure and responses were being obtained from the light source more than  $20^\circ$  out on the perimeter, the receptive field from which responses could be obtained could not be reduced below a diameter of  $10^\circ$ , and the centre of this area could be identified to  $1-2^\circ$ .

Usually when the recording electrode was lowered vertically across the calcarine fissure, responses at first obtained from the lower visual field suddenly changed to the upper field when the electrode had moved a distance of about  $200-300\ \mu$ . Such 'reversals' of the receptive field were found, when the histological sections became available, to have occurred as the calcarine fissure was crossed. The receptive fields were seldom exactly symmetrical about the horizontal meridian. In the last four experiments the needle tracks crossed the 'head' of the mushroom. This gave either a series of four responses, as in Text-fig. 2*B*, or a series of points as in Text-fig. 3*B*, depending on the exact relation of the track to the surfaces of the calcarine cortex. The latency could be reduced to about 30–35 msec by increasing the strength of the stimulus (Text-fig. 1).

Changes in polarity of the first response can be obtained with a small light spot, by shifting the position of the spot over a few degrees. These changes were most marked when the needle was crossing a layer of area 17 obliquely. The distribution of potentials set up by illuminating small visual fields seems to be more complex than when the visual field is diffusely illuminated and area 17 is excited uniformly. On a few occasions single-cell responses were seen. They have conformed to the usual pattern of 'on' and 'off', 'on', or 'off' responses. Early responses have been elicitable from circumscribed areas on the perimeter of  $1-2^\circ$  in diameter near the fovea, and up to  $10^\circ$  across in the peripheral field. No obvious differences in the receptive fields have been seen when leading from the different layers of the cortex, though very obvious differences were detected in the deeper layers of the colliculus in rabbits (Hamdi & Whitteridge, 1953) and the optic tectum of the pigeon (Hamdi & Whitteridge, 1954).

In addition to these early responses, with a latency of 30–60 msec, late responses or a train of responses were frequently seen. These were always obtainable from a much wider area on the perimeter, even at times from the ipsilateral visual field. They have not been systematically studied (Text-fig. 1).

The further the needle tracks were placed laterally, the nearer the receptive fields were to the horizontal meridian. A number of needle tracks were found to run close to the boundary between areas 17 and 18, a boundary which is quite unmistakable in sections. No visual responses



were obtainable from areas 18 or 19, which were frequently traversed by needle tracks which entered just in front of or behind the lunate sulcus.

When the needle tracks lay in area 17 near to the boundaries between areas 17 and 18, the receptive field was always close to the mid line, i.e. in sectors 90–105° and 255–270° (Text-fig. 3).

### *The ipsilateral representation*

In one baboon there was a cataract in the contralateral eye, and the ipsilateral eye was used instead. As the bridge of the nose is very flat, the nasal field of the ipsilateral eye extends almost as far as does the temporal field. No difference in the magnification factor was found in the ipsilateral eye from the pooled results from all eyes. So far both eyes have not been studied simultaneously beyond the foveal region, nor has the region of the blind spot been specially examined.

### *The magnification factor*

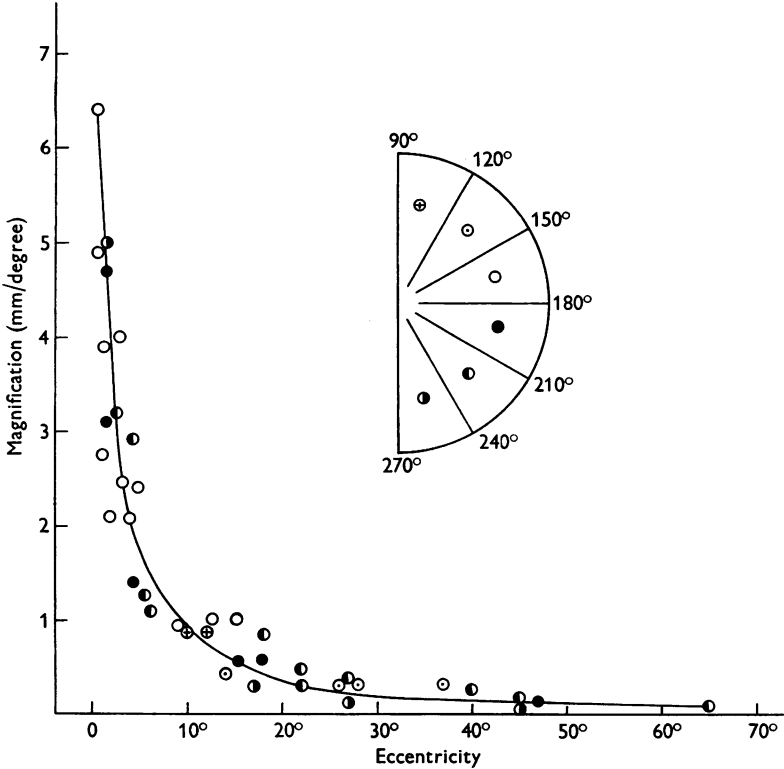
The angular distance apart of two receptive fields and the linear distance between the corresponding points on the calcarine cortex were measured. The magnification factor was obtained as millimetres of cortex concerned with 1° of visual field, by dividing the linear distance by the corresponding angle. The data from all experiments are given in Text-fig. 4, in which the data for six segments, each of 30°, have been plotted separately. There is no significant difference between the six groups of points and one can therefore conclude that there is no significant difference between magnification factors for different radii in the monkey. The magnification factor measured radially over a small distance was found not to differ significantly from the magnification factor measured along the corresponding circumference. No simple equation has been found to fit the data. Neither plotting the data on a semi-log. basis nor plotting reciprocals of the data gives a straight line (Text-fig. 8).

If in fact the magnification factor is the same at all points on a semi-circle of latitude in the visual field, and if it has this same constant value along all radii, where they cut this semicircle, the magnification curve should define the area of the visual cortex. The contralateral visual field can be taken as a quarter sphere. This is sufficiently exact for these purposes, as the receptive field continues beyond the points at which it is cut off by eyebrows, etc., in the position of rest of the eyes, and although the visual field extends to 90° out (Chow, Blum & Blum, 1950), the area of cortex devoted to the extreme visual field is probably so small as to be negligible.

One version of the theoretical visual cortex can be constructed from the empirical data by multiplying the length of each semicircle of latitude by the appropriate magnification factor, and then taking any one meridian—

say the horizontal meridian—and multiplying the angular distances between neighbouring semicircles of latitude along it by the appropriate mean value of  $M$ .

If we give, say, unit radius to the quarter sphere representing the visual field, then an increment of  $1^\circ$  in polar angle (measured from the fixation point) will correspond to an arc on the quarter sphere of length  $\pi/180$ , and



Text-fig. 4. The magnification factor plotted against eccentricity. The data have been grouped in sectors each of  $30^\circ$ .

will be mapped on to our theoretical visual cortex as an arc of length  $M$  mm. The semicircle of polar angle  $\theta$  will be represented on the quarter sphere by a curve of length  $\pi \sin \theta$ , and as the magnification acts uniformly along the length of this curve, its image in the theoretical visual cortex will be a curve of length

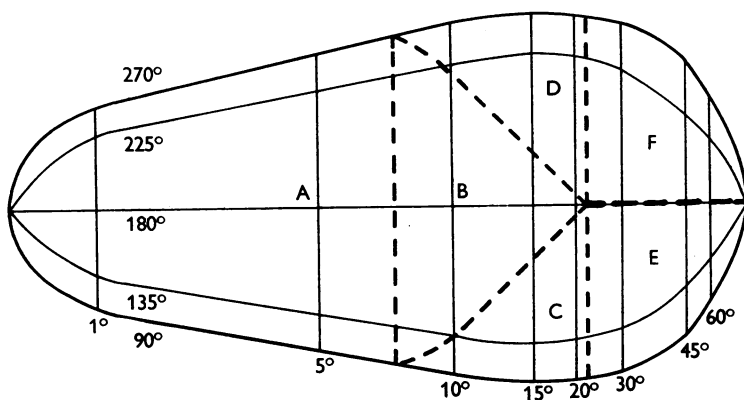
$$M \frac{\pi \sin \theta}{\pi/180} = 180 M \sin \theta \text{ mm.}$$

If  $\theta_1$  and  $\theta_2$  are the polar angles (in degrees) identifying two consecutive semicircles of latitude cutting the basic meridian at  $P_1$  and  $P_2$ , then in the

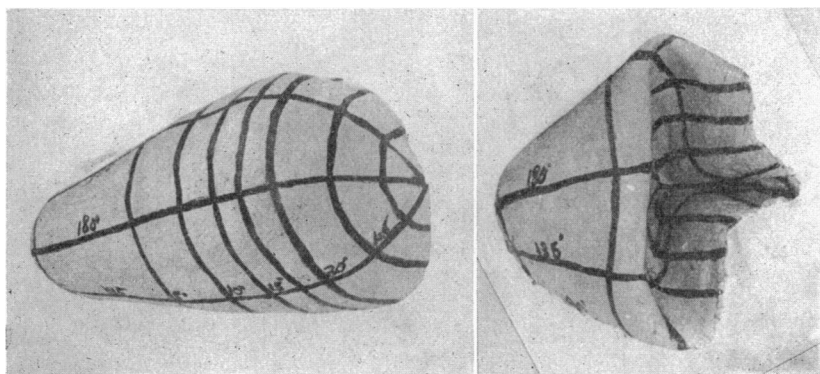
theoretical visual cortex the images of these points will be separated by a distance

$$\frac{M_1 + M_2}{2} (\theta_1 - \theta_2) \text{ mm.}$$

measured along the image of the same meridian. (Here  $M_1$  and  $M_2$  are the magnification factors measured at the polar angles  $\theta_1$  and  $\theta_2$  respectively).

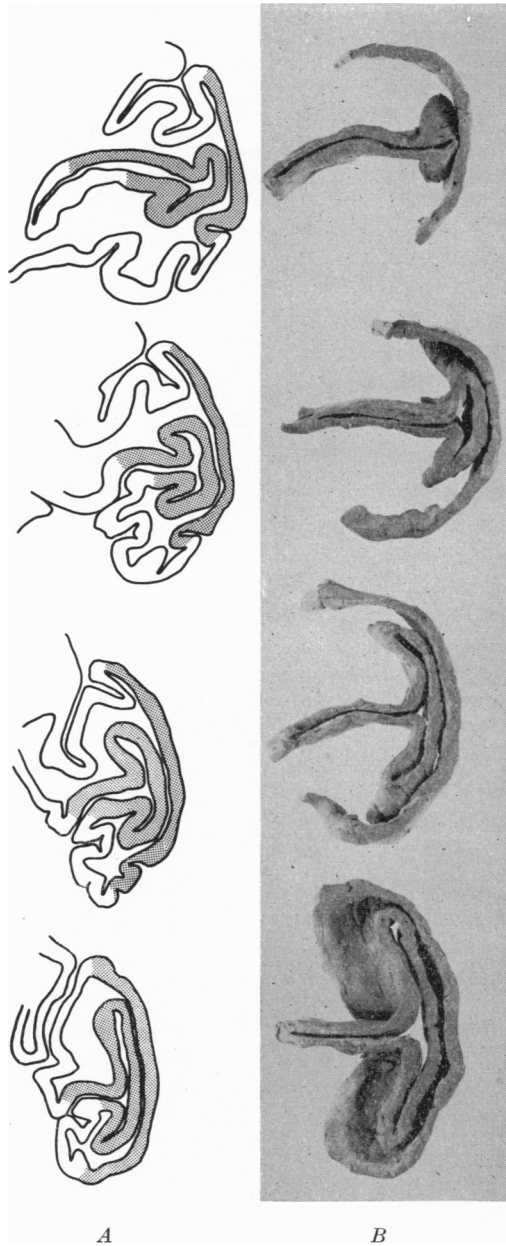


Text-fig. 5. A projection on to a plane of the reconstructed surface for the left hemisphere. Figures refer to the conventional perimeter chart. This surface is folded along the heavy dotted lines so that F touches E, that D and C touch B, and A folds round so that it touches and overlaps the deep surface of B.



Text-fig. 6. Photographs of the model before and after folding. The main horizontal and vertical folds have been completed, but the remainder are only indicated.

This provides the dimensions of a model which can be made in wire covered with paper or cloth and used as a mould for a cast in latex or in 'plasticine'. The cast can then be folded to correspond with the visual cortex (Text-fig. 6). Folding (but not stretching or tearing) will not



Text-fig. 7

*A.* Parasagittal sections, 2 mm apart, of the occipita region of a baboon's brain. Most lateral section above. Most medial section below.

*B.* Parasagittal sections of a 'plasticine' model made and folded as in Text-fig. 5.

affect its validity. It has been found empirically that if two principal folds are made, one horizontal at 25–90° and one vertical at about 8–9°, with the appropriate connecting folds of Text-fig. 5, the resulting folded surface resembles the visual cortex closely. If serial sections are cut of both, the correspondence of the model with the visual cortex can be seen in Text-fig. 7.

The area of the model can be measured by using strips bounded by semicircles of latitude, and has a value of 1320 mm<sup>2</sup>. Various measurements of the area of the visual cortex are given in the literature. That given by Clark (1941) for the macaque is 1445 mm.<sup>2</sup> Another estimate is 650 mm<sup>2</sup>, uncorrected for 70 % linear shrinkage (Chow *et al.* 1950).

#### DISCUSSION

The technical difficulties in producing a self-consistent plot of the visual field on the calcarine cortex have been almost entirely due to unwanted eye movement. Adequate curarization of an animal kept under full general anaesthesia has been by far the best way of avoiding small movements, and constant checking of the visual fixation by means of a fixed electrode left on the cortex at the foveal representation provides an adequate safeguard. No doubt more accurate mapping could have been attained by leading only from single units in the cortex. It is, however, essential to lead from a very large number of points in each experiment to obtain a useful map, and the time available while the animal remained in good condition made multiunit recording inevitable. This results in leading from larger areas without sharply defined edges, but as the centre of the receptive area can be defined to 1° or less, it causes no serious difficulty.

The density of the degeneration produced in the lateral geniculate body both by small retinal lesions (Clark & Penman, 1934) and by small cortical lesions (Polyak, 1957) suggests that geniculate-ganglion cells and also cortical cells having adjacent or overlapping receptive fields must be closely adjacent. This provides some further justification for using large electrodes which pick up the summed effects from many cells. Direct mapping of receptive fields of adjacent cortical nerve cells has been achieved on one occasion. All the fields seen were overlapping. In the monkey's lateral geniculate body such receptive fields have also been found to overlap (P. M. Daniel, K. N. Seneviratne and D. Whitteridge, unpublished).

The errors involved in the estimation of magnification factors are not negligible. Measurement of the distance between points in the visual field has an error of 10 % at least, and measurement of the distance between

corresponding points on the cortex has difficulties arising from uncertainties due to leading from different points in the thickness of the cortex, especially when this has been crossed obliquely. There are also errors in measurement of sections caused by unequal shrinkage. Nevertheless, the points obtained make it obvious that there is a relationship between cortical magnification and eccentricity (Text-fig. 4). Talbot & Marshall (1941) suggest in their text that this is a discontinuous relation but their Fig. 5 makes it clear that the relation is a continuous one.

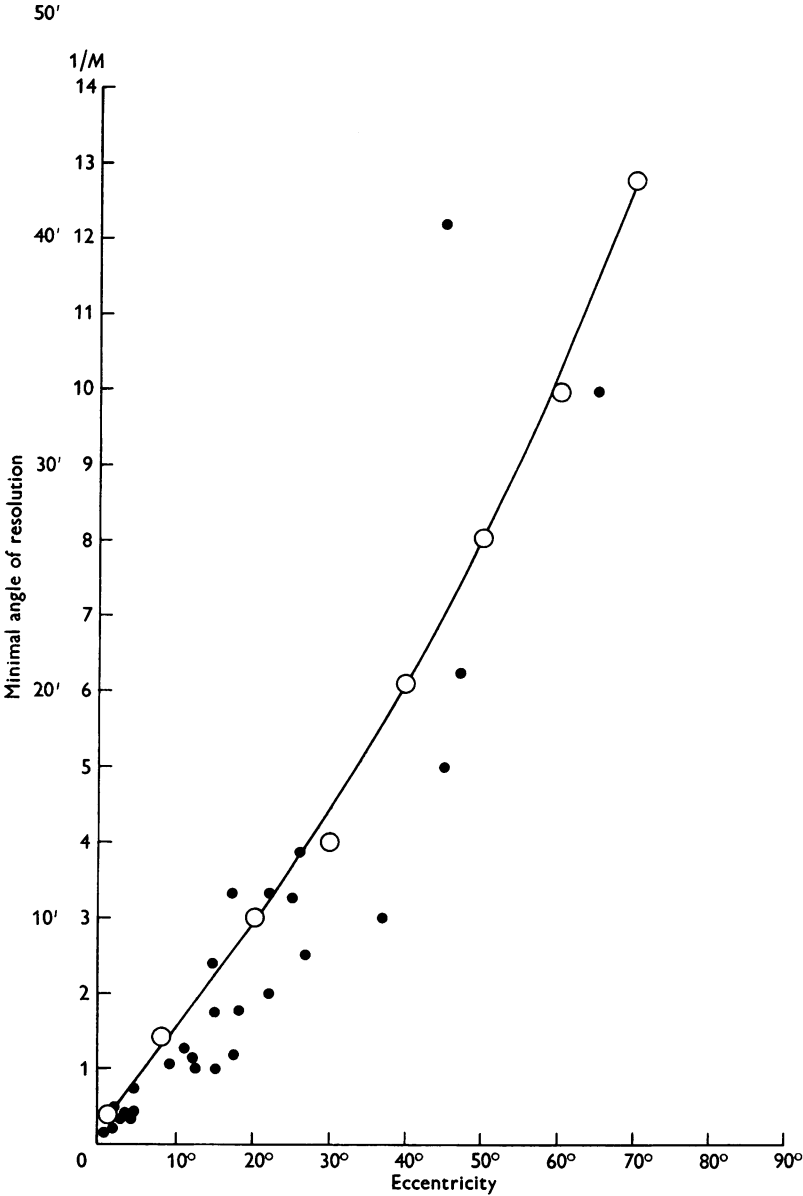
The only assumption which is required in order to calculate the area of the visual receptive field from measurements of cortical magnification is that the magnification depends only upon the distance from the fovea and, at any point, is the same for all directions. If all the data are grouped into six sectors each of  $30^\circ$ , as in Text-fig. 4, it seems that there is no appreciable difference between them. However, in the frog, there are large differences between magnification factors measured along horizontal and vertical meridians (Jacobson, 1960) and in the pigeon there is an area of increased magnification corresponding to the anterior end of the horizontal meridian (D. Whitteridge, unpublished observations).

In the monkey, differences in the shape of the visual area of the cortex between the scheme suggested here and the drawing of Polyak (1957, Fig. 259) are not very great. The foveal end of the visual area is, we think, more pointed and the peripheral end more rounded, and the semicircles of latitude appear in a surface projection as straight lines at right angles to the meridians. The boundary of the figure is formed almost entirely by the vertical meridian and the semicircle of latitude for  $90^\circ$  is reduced to a very small strip, in which our model differs considerably from Polyak's drawing.

Some attempt to relate minimal angle of resolution and the distribution of retinal ganglion cells in man has already been made by Weymouth (1958), who points out that both fall off linearly with eccentricity for  $30^\circ$ . There are, unfortunately, no reliable ganglion-cell counts for the peripheral retina. Before we can provide an anatomical basis for the minimal angle of resolution from the retina to the cortex, we need to know if there is multiplication or reduction of cell paths in the lateral geniculate body, and how axons from the lateral geniculate body are distributed to the cortex.

On the first point the data are probably insufficient. Brindley (1960) has quoted figures which suggest that there is multiplication of paths at the lateral geniculate in the monkey and even greater multiplication in the cat, but, on the contrary, a reduction in paths in man and in the rat. Unfortunately, estimates by different authors for the number of cells in the same structure do not agree closely.

Data are less incomplete for the monkey than for other animals. There are 1,210,000 nerve fibres in the optic tract (Bruesch & Arey, 1942) and



Text-fig. 8. The minimal angle of resolution for man (Weymouth, 1958),  $\circ$  ; and values for the reciprocal of the magnification factor for the monkey,  $\bullet$ .

1,590,000 cells in the small-celled layers and 209,000 cells in the large-celled layers of the lateral geniculate body (Clark, 1941). After allowing for fibres in the optic tract which run to the superior colliculus and elsewhere, this certainly suggests that there are more cells in the lateral geniculate body than in the optic tract, and that there may be twice as many. Gleses & Clark (1941) have observed single optic-tract fibres ending on up to 5 cells in the lateral geniculate body, but they do not say whether this observation was made on cells at the posterior pole, which is the macular area, or at the anterior end where the peripheral field is represented. On the crucial point, therefore, whether central and peripheral fibres behave in the same way or in different ways at the lateral geniculate body, there is insufficient evidence.

For the optic radiations the situation is clearer. Clark (1941) suggests that there is an even distribution of 1350 fibres/mm<sup>2</sup> to area 17.

Sections of different parts of area 17 are remarkably uniform in appearance, though Chow *et al.* (1950) find 148 cells/0.001 mm<sup>3</sup> on the posterolateral (macular) area as against 178 cells/0.001 mm<sup>3</sup> in the medial (peripheral) areas. Unfortunately the area of distribution of dendrites from single axons of the optic radiation is not known in the monkey. In the cat this extends to 650  $\mu$  diameter, so that one axon can make synaptic contact with some 5000 cells (Sholl, 1956).

From our own experimental data on the monkey, 1° at the fovea occupies about 6 mm linearly on area 17 of the cortex (Text-fig. 4). This is a considerably smaller figure than that given by Talbot & Marshall (1941) of 2'/mm, or 30 mm/degree. Central visual acuity has been measured for macaques by Grether (1941), who gives a minimal angle of resolution of 0.67'. This must correspond to a cortical distance of 67  $\mu$  in the area of foveal representation, or the distance occupied by about five cells in the densest part of layer IV of the cortex. So far there are no data available for the peripheral visual acuity in the monkey. It is, however, interesting to observe that magnification in the monkey and visual acuity in man both fall off in a very similar way in the peripheral field. In Text-fig. 8 the reciprocal of the magnification factor in the monkey has been plotted against minimal angle of resolution in man. While this way of plotting magnification minimizes the scatter of values at small angles and exaggerates it at large angles, there is reasonable agreement between the two sets of data. If, in fact, the peripheral visual acuity in the monkey does fall off as it does in man, it would follow that the minimal angle of resolution would correspond to about 67  $\mu$  on the cortex of the monkey, both for the foveal area and for the extreme periphery. Presumably two peaks of excitation would have to be separated by this distance and by a corresponding number of cortical cells for them to give rise to separate sensations.



Although the essential information on the magnification factor in man is lacking, there are interesting points of comparison. The total area of the calcarine cortex is about 3000 mm<sup>2</sup>, or about twice that of the monkey, but the cell density is not greater than half (Shariff, 1953). This is probably related to the greater number of fibre connexions per unit area (cf. Wright, 1934). The shape of area 17 is probably similar to that in the monkey, though the folding of the cortex is very different. In transverse serial sections the foveal area is difficult to deal with and seems sometimes to have been omitted in studies of the human visual cortex. This is clear in one of the series of occipital lobes measured by Filimonoff (1933), where an apparently isolated sector of area 17 appears on the lateral surface about 1 cm anterior to the posterior pole. It is also clear from Filimonoff's very careful work that a vertical fold similar to that seen in the monkey does occur in man in one brain in three or four. There is, however, usually longitudinal folding on both sides of the vertical fold. In the commoner arrangement the longitudinal fold forming the calcarine fissure runs almost from end to end of area 17 and smaller folds both parallel and transverse are to be found in the depths of the calcarine fissure.

Recently it has been customary to minimize the importance of precise localization in the primary sensory areas. This has arisen partly from experiments of Lashley (1939) on the surviving ability of rats to acquire visual discrimination when all but a remnant of the visual cortex containing 700 geniculostriate cells in 1.5 mm<sup>2</sup> of cortex had been removed. This has been generalized into the statement that the visual area as a whole has some slight 'action propre', but not its parts (Boring, 1960). Insufficient attention seems to have been paid in interpreting these experiments to the rat's poor visual acuity, and the extent to which a very restricted visual field can be used by moving the head. The conclusions of Doty (1958) that localization in the cat's visual cortex was not precise, apply to the later cortical waves and not to the earlier responses, which are sharply defined and can be mapped in a point to point manner (D. Whitteridge, unpublished observations).

On the other hand, the classical observations of Holmes (1919) showed that sharply defined cortical lesions produce sharply defined scotomata with edges separating areas of normal acuity from areas of total blindness. The work of Hubel & Wiesel (1959) suggests that point-to-point representation on the cortex is an essential preliminary to the analysis of patterns by selective activation of cortical cells. According to Maturana, Lettvin, McCulloch & Pitts (1960) the corresponding process in the frog's tectum is carried out largely by retinal cells specifically sensitive to particular contours, but again a point-to-point representation on the corresponding surface in the central nervous system is present. In addition, more diffuse

mechanisms seem to be involved in the cortical responses of longer latency, but little is yet known of their afferent paths.

#### SUMMARY

1. The representation of the visual field on the calcarine cortex in baboons and macaques has been determined by means of long steel electrodes of less than  $10\ \mu$  tip and small visual stimuli subtending  $10'$  of arc at the eye.

2. The magnification factor, i.e. the linear extent of cortex concerned with each degree of visual field, has been determined. At the foveal region the minimal angle of resolution occupies an area of the cortex of about  $67\ \mu$  in diameter.

3. The magnification factor appears to be the same for all points on a semicircle of latitude, and for small angles of displacement in the visual field it appears to be independent of the direction in which the displacement is taken.

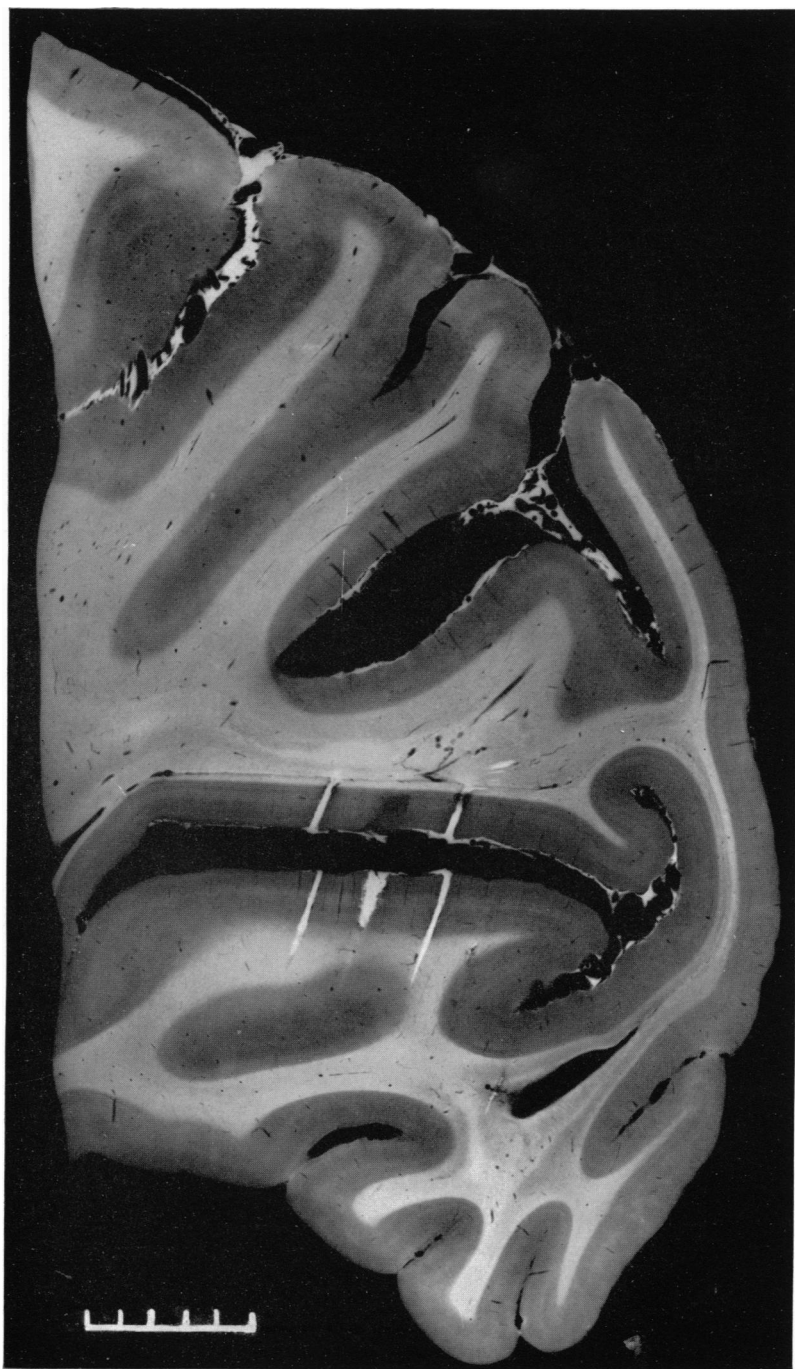
4. From these data a surface can be calculated which can be folded to give a close approximation to the size and folding of the visual cortex.

5. The applicability of these results to man is discussed.

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## EXPLANATION OF PLATE

A parasagittal section 100  $\mu$  thick of the baboon's occipital cortex 4 mm from the mid line. Five needle tracks are visible, and are very nearly in the plane of the section. Weil's stain. Scale in mm.